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CAVITY TREE SELECTION BY RED-COCKADED WOODPECKERS IN RELATION TO TREE AGE

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ABSTRACT.—We aged over 1350 Red-cockaded Woodpecker (*Picoides borealis*) cavity trees and a comparable number of randomly selected trees. Resulting data strongly support the hypothesis that Red-cockaded Woodpeckers preferentially select older trees. Ages of recently initiated cavity trees in the Texas study areas generally were similar to those of cavity trees initiated during the last several decades. In effect, the birds are continuing to select the oldest trees from a pool of trees of increasing age. This suggests that the current average age of cavity trees on these sites (85–130 yrs) may not provide optimum cavity trees for this endangered species. *Received 15 July 1990, accepted 27 March 1991.*

The Red-cockaded Woodpecker (*Picoides borealis*) is an endangered species endemic to pine forests of the southeastern U.S. (Jackson 1971). Deforestation and alteration of remaining forest habitat have severely affected Red-cockaded Woodpecker populations; current populations are isolated, and most are declining (Jackson 1971, Lennartz et al. 1983, Conner and Rudolph 1989, Costa and Escano 1989).

It has been generally accepted that Red-cockaded Woodpeckers select older pines for cavity excavation (e.g., Jackson 1971, Jackson et al. 1979, Locke 1980). Average ages of Red-cockaded Woodpecker cavity trees range from 62–149 years (Lennartz et. al. 1983, Hovis and Labisky 1985, Conner and O'Halloran 1987, DeLotelle and Epting 1988, Hooper 1988).

Several hypotheses have been suggested to account for the selection of older pines as cavity trees by Red-cockaded Woodpeckers (Beckett 1971, Conner and Locke 1982, Jackson and Jackson 1986). Red heart fungus (*Phellinus pini*) decays the heartwood of living pines and facilitates the excavation of cavities by Red-cockaded Woodpeckers (Jackson 1977a, Conner and Locke 1982). *P. pini* incidence increases with tree age, and southern pine species younger than 60 years are rarely infected (Nelson 1931; Wahlenberg 1946, 1960; Hepting 1971). Consequently, the hypothesis that Red-cockaded Woodpeckers select older trees with red heart decay, or at least an increased probability of decay, has received considerable support.

An additional series of hypotheses relate to the correlation between tree age and size. Older and larger trees allow cavities to be placed at greater

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heights. The presence of sufficient heartwood and red heart decay at greater heights are the primary controlling factors. Cavities at greater heights may experience less predation (Jackson 1974, Conner and O'Halloran 1987), less fire damage due to igniting of resin (Conner and Locke 1979), and less girdling of trees at cavity due to woodpecker excavations (Jackson 1985). The decreasing availability of suitable old trees has been hypothesized as a major contributing factor in the decline of the species (Steirly 1957, Ligon 1970, Jackson 1971, Jackson et al. 1979, Lennartz et al. 1983).

In a recent comment, Field and Williams (1985) focused attention on the limited data supporting the conclusion that old pines are a critical feature of Red-cockaded Woodpecker habitat. Field and Williams were able to locate only seven studies that provided data on the ages of cavity trees and potentially available trees. Several of these studies, because they were not specifically designed to address the question of cavity tree age, are of limited applicability. Subsequent studies (Hovis and Labisky 1985, Conner and O'Halloran 1987, DeLotelle and Epting 1988, Hooper 1988) have substantially rectified this situation.

Although the use of older relict trees by Red-cockaded Woodpeckers is now well established, the issue of preferred age has not been investigated previously. Most forests currently occupied by Red-cockaded Woodpeckers are relatively young (<150 yrs) with a low frequency of older relict trees. We hypothesize that although Red-cockaded Woodpeckers currently select cavity trees from among the oldest trees available, the age distribution available is not sufficient to provide potential cavity trees of the preferred ages. Three scenarios exist for the selection of older cavity trees by Red-cockaded Woodpeckers: (1) a threshold tree age exists beyond which the birds are not selective, (2) an optimum tree age exists, and (3) the birds select the oldest trees available.

During the course of extensive Red-cockaded Woodpecker surveys on U.S. Forest Service land in Texas, we collected extensive data on ages of Red-cockaded Woodpecker cavity trees. We also collected age data on non-cavity trees for comparative purposes. These data provide additional insight into the selection of potential cavity trees by Red-cockaded Woodpeckers and allow a partial test of the above hypothesis.

STUDY AREAS AND METHODS

The study was conducted on the Angelina (62,423 ha), Davy Crockett (65,359 ha), and Sam Houston (65,218 ha) National Forests located in eastern Texas. The Davy Crockett (DCNF), Sam Houston (SHNF) and northern portion of the Angelina (ANF) National Forests are comprised of pine and mixed pine-hardwood stands on the uplands and mixed hardwood stands on the bottomlands. Loblolly pine (*Pinus taeda*) and shortleaf pine (*P. echinata*) predominate, and longleaf pine (*P. palustris*) is extremely rare. The southern portion of the ANF is similar except that the dominant pine is longleaf, and upland hardwoods are less frequent. Detailed descriptions of the ANF and DCNF study areas can be found in Conner and Rudolph (1989).

Recent surveys (Rudolph and Conner 1988, Conner and Rudolph 1989) provide Red-cockaded Woodpecker population data for these forests. The ANF and DCNF each support fewer than 30 active clusters (colonies in past literature, see Walters et al. 1988), and are declining. The SHNF supports 130+ active clusters, and the current population trend is unknown. In addition, numerous inactive clusters are present on each forest.

Location data for all known Red-cockaded Woodpecker clusters on Texas National Forests were obtained from the Forest Supervisor's office in Lufkin, Texas. We visited cluster sites on the DCNF and SHNF during 1987–1988. Cluster sites on the ANF were visited between 1983 and 1988.

Cavity trees were located and a 5-mm diameter increment core was extracted from each tree at breast height. A binocular dissecting scope was used to count annual growth rings. A correction factor (three years for loblolly and shortleaf, five years for longleaf) was added to each core count to allow for initial growth to breast height. Pine species, cavity tree status (active or inactive) (Jackson 1977b, 1978), and number of cavities and cavity starts were recorded for each tree.

Examination of cavity trees and existing records indicated that most have been cavity trees for several to many years. However, a subset of cavity trees was judged to have been initiated recently as cavity trees based on four criteria: (1) currently active, (2) lack of a developed plate around cavity entrance (Jackson and Jackson 1986), (3) lack of an extensive resin well system, and (4) lack of additional cavities not meeting these criteria. Although a specific length of time since these trees were first initiated as cavity trees cannot be established, as a group they should represent the most recently established cavity trees in these populations. Sequential observations, especially on the ANF, indicate that once cavity excavation is complete most trees fail to meet the above criteria within 1–2 years.

Data were collected from non-cavity trees in areas adjacent to Red-cockaded Woodpecker clusters. A mature timber stand between 150 m and 750 m from each cluster was chosen based on overall similarity to cluster stands. Availability of suitable stands determined the degree of similarity. Trees within these stands were randomly selected (N = number of cavity trees in adjacent clusters) by rotating a spinning device and selecting the nearest tree in the direction indicated. Differences in final sample size (Table 1) were due to slight variation in species composition and number of cores unusable due to decay. Random trees were chosen subject to a size restriction ($\geq$30 cm DBH) and inclusion in the canopy, criteria that cavity trees rarely violate.

Data were also collected from a sample of non-cavity trees within stands containing clusters using the same methods as for random trees. Clusters sampled were on the DCNF (loblolly and shortleaf) and ANF (longleaf). Clusters containing $\geq$eight cavity trees and one or more recently initiated cavity trees were selected for sampling of non-cavity trees.

RESULTS

Data were obtained on 1368 cavity trees and 1355 random trees (exclusive of random non-cavity trees within clusters). Mean ages (years) of cavity trees were 131.1 for longleaf pine, 90.0 for loblolly pine, and 104.2 for shortleaf pine. Significant differences were detected between mean ages of all three species of cavity trees (ANOVA, $P < 0.001$; Duncan's Multiple Range test, $P < 0.05$).

Mean ages of cavity trees were significantly greater (18.7–68.2 years)

TABLE 1
AGE OF RED-COCKADED WOODPECKER CAVITY TREES AND RANDOM TREES (150–750 M) FROM CLUSTERS ON THREE NATIONAL FORESTS IN TEXAS

Forest	Species	Type	N	Mean	Range	SD	P^a
Angelina	*Pinus palustris*	Cavity	149	130.0	49–332	45.5	
		Random	157	61.8	38–169	21.7	<0.001
	P. taeda	Cavity	45	87.0	52-112	16.1	
		Random	50	66.8	28–107	16.9	<0.001
	P. echinata	Cavity	20	100.5	86–132	11.1	
		Random	28	70.8	44–110	16.4	<0.001
Davy Crockett	*P. taeda*	Cavity	151	96.5	66–156	13.1	
		Random	97	70.8	35–111	18.1	<0.001
	P. echinata	Cavity	190	105.1	63–169	16.6	
		Random	170	85.6	51–165	19.1	<0.001
Sam Houston	*P. taeda*	Cavity	728	88.7	49–133	14.2	
		Random	658	70.0	32–123	14.7	<0.001
	P. echinata	Cavity	85	103.4	54–125	14.8	
		Random	195	82.9	51–124	18.1	<0.001

[a] One-tailed *t*-test.

than those of random trees distant from clusters in all cases, regardless of tree species or National Forest (Table 1).

In 11 of 14 cases, cavity trees were significantly older than non-cavity trees within the same stand (Table 2). Mean ages of cavity trees ranged from 2.6–33.9 years older than random trees within these stands. The three exceptions involved shortleaf pine in stands containing few younger trees. These combined data were also analyzed by means of one-way and two-way ANOVA. Significant differences were found between cavity tree ages and non-cavity tree ages ($P < 0.001$), indicating that the differences transcend tree species and stands.

A total of 140 cavity trees were identified as recently initiated by the criteria listed above. The ages of these trees were compared to those of all other cavity trees. In five of the seven cases, there was no significant difference between the mean age of recently initiated cavity trees and all other cavity trees (Table 3). The two significant comparisons involved loblolly pine on the DCNF and SHNF. Mean ages of recently initiated cavity trees were 13.5 and 6.2 years younger, respectively, than all other cavity trees in these two significant cases ($P < 0.001$).

DISCUSSION

Our results indicate clearly that Red-cockaded Woodpeckers select older pines for cavity excavation. This preference is maintained for each of the three pine species used in Texas and on three different national forests.

TABLE 2

AGE OF RED-COCKADED WOODPECKER CAVITY TREES AND NON-CAVITY TREES WITHIN STANDS ON THREE NATIONAL FORESTS IN TEXAS

Species	Cluster	Type	N	Mean	Range	SD	P^a
Pinus palustris	3	Cavity	10	110.2	83–175	28.7	
		Non-cavity	10	76.3	48–98	18.5	<0.01
	4	Cavity	9	95.1	80–105	7.3	
		Non-cavity	10	78.7	44–100	23.3	<0.05
	5	Cavity	6	109.8	81–148	26.4	
		Non-cavity	20	84.7	76–95	5.6	<0.05
	6	Cavity	6	97.3	86–103	6.5	
		Non-cavity	10	87.2	61–101	11.1	<0.05
	7	Cavity	8	104.6	89–126	13.2	
		Non-cavity	10	89.2	71–106	11.8	<0.01
	8	Cavity	6	111.8	100–149	18.5	
		Non-cavity	15	93.0	80–102	5.7	<0.05
P. taeda	1	Cavity	5	86.8	69–107	17.1	
		Non-cavity	5	69.2	49–76	11.3	<0.05
	2	Cavity	6	99.2	96–103	3.1	
		Non-cavity	9	75.6	68–86	5.4	<0.001
	9	Cavity	3	111.3	110–113	1.5	
		Non-cavity	8	95.0	74–106	11.3	<0.01
P. echinata	2	Cavity	7	106.3	74–154	25.4	
		Non-cavity	11	73.2	60–80	5.9	<0.001
	9	Cavity	5	98.4	91–111	8.4	
		Non-cavity	10	99.7	88–112	7.1	N.S.
	10	Cavity	5	104.6	98–113	5.6	
		Non-cavity	10	99.2	87–110	6.6	N.S.
	11	Cavity	4	108.3	104–113	4.0	
		Non-cavity	10	99.6	91–108	5.4	<0.01
	12	Cavity	13	118.6	107–130	7.2	
		Non-cavity	10	116.0	108–122	4.9	N.S.

[a] One-tailed *t*-test.

This result is consistent with previously published studies (Lennartz et al. 1983, Hovis and Labisky 1985, Conner and O'Halloran 1987, DeLotelle and Epting 1988, Hooper 1988).

Even within stands the selection of older pines is also apparent. That the age of cavity trees was significantly greater than that of non-cavity trees within stands suggests that selection is based on individual trees and not on selection of older stands. The three exceptions were situations that provided minimal opportunity for selection based on age. The average ages of trees in these stands (99.2–116 years) included three of the four oldest averages among stands examined, and the ranges of tree ages were

TABLE 3
AGE OF RECENTLY INITIATED AND ALL OTHER RED-COCKADED WOODPECKER CAVITY TREES ON THREE NATIONAL FORESTS IN TEXAS

Forest	Species	Type	N	Mean	Range	SD	P[a]
Angelina	*Pinus palustris*	all other	136	130.8	49–332	46.2	
		recently initiated	13	122.2	80–200	37.8	N.S.
	P. taeda	all other	42	87.7	52–112	16.0	
		recently initiated	3	76.7	62–97	18.2	N.S.
	P. echinata	all other	19	100.7	86–132	11.4	
		recently initiated	1	96.0	96	0.0	N.S.
Davy Crockett	*P. taeda*	all other	137	97.7	66–156	12.5	
		recently initiated	16	84.2	69–108	12.3	<0.001
	P. echinata	all other	158	105.0	63–169	16.6	
		recently initiated	30	105.7	74–161	17.2	N.S.
Sam Houston	*P. taeda*	all other	652	89.3	49–133	14.0	
		recently initiated	68	83.1	59–120	15.1	<0.001
	P. echinata	all other	72	104.6	64–125	12.7	
		recently initiated	9	98.1	59–120	21.2	N.S.

[a] One-tailed t-test.

narrow. A similar pattern has been reported by DeLotelle and Epting (1988).

Cavity tree selection by Red-cockaded Woodpeckers is a complex process. Tree diameter, presence of redheart fungus, heartwood diameter, bole length, growth history, and resin characteristics have all been demonstrated to vary between cavity trees and non-cavity trees (Jackson 1977a, Jackson et al. 1979, Conner and Locke 1982, Hovis and Labisky 1985, Conner and O'Halloran 1987, Hooper 1988). In addition, stand characteristics, including basal area, midstory development, and canopy height, have been demonstrated to vary between cluster stands and non-cluster stands (Hooper 1988, Locke et al. 1983, Hovis and Labisky 1985, Conner and O'Halloran 1987, Conner and Rudolph 1989). Correlations between these variables and tree age are common. Consequently, a multiplicity of factors is available as a basis for cavity tree selection by Red-cockaded Woodpeckers. Conner and O'Halloran (1987) have presented evidence suggesting that individual tree characteristics are more important than stand characteristics. The specific criteria used by Red-cockaded Woodpeckers in choosing cavity trees are unknown. However, the ultimate result, that older trees are selected, is well documented.

Questions relating to the preferred age of cavity trees are more difficult to answer. Our data, analyzed by forest and by species, indicate that in most cases there is no significant difference between mean ages of recently initiated cavity trees and all other cavity trees. Jackson et. al. (1979) and Hovis and Labisky (1985) have previously reported average ages for recently initiated cavity or start trees (variously defined). Although average ages were not compared to other cavity trees statistically, their data suggest that average ages of recently initiated trees are similar to those of all cavity trees.

Engstrom and Evans (1990) have recently presented data suggesting that even in an old growth longleaf pine stand, Red-cockaded Woodpeckers are selecting the older trees from among those available. Two additional data sets also indicate use of very old trees. Teitelbaum and Smith (1985) reported estimated cavity tree ages in excess of 150 years for loblolly pine and 300 years for longleaf pine, based on an age-diameter relationship determined for non-cavity trees. We recently confirmed these ages by coring the actual cavity trees. Hedrick (unpubl. data) reports a mean age of 189 years for longleaf pine cavity trees in the Oakmulgee District of the Talledega National Forest. Maximum age was 368 years for an active cavity tree.

Our conclusion from this pattern is that as the regenerating forests in Texas continue to age from the initial logging 70–100 years ago (Maxwell and Baker 1983, Conner and O'Halloran 1987), Red-cockaded Woodpeckers are continuing to select cavity trees from the older available trees. The preferred age of cavity trees may be greater than the current age structure of the three forests provides. Consequently, the birds continue to select cavity trees from the older available trees with the result that the average of recently initiated cavity trees tracks the increasing age of the available trees. The data support our initial hypothesis that the tree age distribution available is not sufficient to provide potential cavity trees of the preferred ages. Our data also indicated that scenario (1), a threshold age beyond which the birds are not selective, is not operating. However, our data are not sufficient to differentiate between scenarios (2) and (3). This question can only be answered with data from older forests.

Significant age differences were detected between recently initiated cavity trees and all other cavity trees in the two cases of loblolly pines on the Davy Crockett and Sam Houston National Forests. This suggests that for this species, tree ages have advanced sufficiently to allow separation to develop between the age distributions of recently initiated cavity trees and all other cavity trees. That this has occurred in loblolly rather than shortleaf or longleaf pines is consistent with several characteristics of loblolly pine compared to other species. Loblolly pines are characterized by faster growth (Wahlenberg 1946), shorter lifespan (Platt et al. 1988), and presence of more heart rot at younger ages (Nelson 1931; Wahlenberg 1960, pers. obs.) than the other species. Consequently, the optimum or suitable ages of loblolly pines for Red-cockaded Woodpecker cavity trees may be considerably younger than for the other pine species. Reported ages of cavity trees of the three species considered here are generally oldest for longleaf and shortleaf pine and youngest for loblolly pine (e.g., Wood 1975, Jackson et al. 1979, Jackson and Jackson 1986).

Several data sets now exist that support the hypothesis that Red-cockaded Woodpeckers select old pines as cavity trees. The existence of a threshold age of 60–80 years is also indicated by these data sets (DeLotelle and Epting 1988, Hooper 1988). The incidence of cavity trees of younger age is rare. Tree species, availability of older trees, incidence of heart rot, etc. influence the average age of cavity trees but do not greatly affect the minimum age.

Above the threshold age, the suitability of pines as potential cavity trees presumably increases. This increase is suggested by several of the data sets and is strongly supported by the data presented above. However, these data only apply to a limited age span above the threshold age due to the current rarity of pine stands of advanced age (i.e., those with significant numbers of trees in excess of 100 years). The shape of a suitability curve may plateau, peak, or continue to increase with increasing tree age. Current data are insufficient to distinguish among these alternatives.

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